David Hubel Retrospective

Charles D. Gilbert[1]
Laboratory of Neurobiology, The Rockefeller University, New York, NY 10065

> *E volta nostra poppa nel mattino de' remi facemmo ala al folle folo*
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> Dante, *Inferno* XXVI, 123
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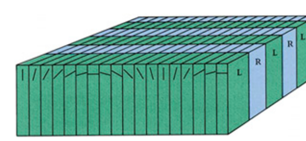
> ("And having turned our stern unto the morning, the oars made wings for our mad flight," translated from a plaque given to Hubel and Wiesel by their friend, Elio Raviola)

David Hubel, noted neuroscientist and Nobel laureate, died on September 22th at the age of 87. In his collaboration with Torsten Wiesel that lasted several decades, David unlocked the door to understanding the transformation of visual information performed by the visual cortex. At the time Hubel and Wiesel began their studies, the emergent properties of sensory cortex were a mystery. The central concept of sensory processing, first defined by Sir Charles Sherrington, is the receptive field, the area of the sensory surface within which the appropriate stimulus could activate a neuron. At early stages in the visual pathway any given neuron's receptive field is a small window on the visual scene. The question that bedeviled neuroscientists at the time was: What is the optimum visual stimulus to put within the receptive field to get neurons to respond? Hubel and Wiesel found, through a fortuitous event in their search for the "code" of the visual cortex, that cortical neurons were selective for the orientation of line segments placed within their receptive fields. This discovery provided the first insight into how the visual cortex begins to analyze the contours that describe an object's shape.

David Hubel (*Left*) and Torsten Wiesel (*Right*) after receiving news of the 1981 Nobel Prize in Medicine. Photo courtesy of Harvard University, Joe Wrinn, photographer.

David gravitated toward thinking of the brain in geometric terms. He was in a sense an architect of the brain. Hubel and Wiesel found that the property of orientation preference was organized in a columnar fashion, where across the cortical layers, from the surface of the visual cortex to the white matter, neurons had the same orientation preference, and as one moved parallel to the cortical surface there was a regular clockwise or counterclockwise shift in orientation preference, with the full range of orientations cycling over the cortical surface with a periodicity of about 1 mm. Along with orientation preference, neurons put together input from the two eyes, leading to the property of ocular dominance, which is also organized in a columnar fashion. From this columnar organization David produced an "ice cube" model of the functional architecture of visual cortex, a schematic representation of a cortical unit that tiles across the cortex to analyze the visual field in all attributes of form, depth, color, and movement. Later, David worked with Marge Livingstone to continue this theme, finding additional elements of the functional architecture of the visual cortex that mediate the parallel processing of color, form, and movement. It is not surprising that geometry governed David's leisure activities: he loved to shape geometric solids with the lathe and was a skilled wood worker, having built much of the furniture in his house. Even David's love of music—he played the piano and flute—tended toward the patterned organization of baroque compositions. For David, the structural regularity of the brain was the best evidence for the cortical algorithm; one didn't need statistics or any level of proof beyond showing the crystalline organization of cortical functional architecture.

David Hubel in his lab in the mid-1960s, from Torsten Wiesel's collection.



Hubel's "Ice Cube" model of the functional architecture of the visual cortex from Hubel DH (1988) *Eye, Brain and Vision* (Scientific American Library, New York).

The second important leg of the Hubel and Wiesel opus is their work on the critical period. During the early postnatal period, alteration in visual experience from either eye alters the balance of visual inputs to binocular cortical cells. This alteration is in part because of the expansion or contraction in the size of axonal arbors coming from the lateral geniculate nucleus to the visual cortex. The capacity for cortical plasticity, at least for the property of ocular dominance, is limited to the first few months of postnatal life, a span of time known as the critical period. The implications of these findings are profound: it means that for children born with cataracts, the cataract must be removed before the end of the critical period in order for normal connections from the eye to the visual cortex to be established. The findings also led to a widespread belief that early experience was required for normal brain development, and was an impetus for developing programs of early childhood education.

For David, doing science was the ultimate pleasure. He loved to work with his hands, and his design of an electrode for recording from single neurons in the intact brain made possible all of the discoveries that followed.

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[1]E-mail: gilbert@rockefeller.edu.

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For David, the pursuit of science was a personal, hands-on experience, and he left the students and postdoctoral scholars in his laboratory to work on their own independent lines of research, working himself with only one or, on occasion, two collaborators at a time. He avoided getting entangled in administrative responsibilities, and encouraged his younger colleagues to act similarly, to achieve the ultimate goal of making new scientific discoveries. However, David did see the value of engaging the public in understanding the value and the beauty of science. For him it was important for the public to understand the great value of animal research for the sake of knowledge and of human health. David was a great communicator. It was a pleasure to hear the clarity of his presentations, of his own work, in the courses he taught, and in the finely crafted papers that became hallmarks of the early history of neural systems research. As a result, David attracted a diverse group of physicists, mathematicians, and biologists into the field. On a personal level, his wry and irreverent sense of humor created a fun, collegial environment in the Neurobiology department at Harvard Medical School, where everyone felt like an equal, students and professors alike. David's approach to science was a guiding light for younger generations of neuroscientists and his legacy will be a lasting one.